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Growth delay by winter precipitation could hinder *Juniperus sabina* persistence under increasing summer drought

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ABSTRACT

Plants in Mediterranean mountains are particularly vulnerable to climatic change. In these environments, low temperature is combined with water shortage during summer, and as a result, the positive effect of global warming theoretically expanding the growing season length may be counterbalanced by rising drought stress. These circumstances may be exacerbated in the rear edge of species distribution, where warmer conditions occur. Here, we examined the climate-growth relationships of *Juniperus sabina*, a major prostrate shrub above the treeline in Mediterranean mountains, to investigate climate sensitivity and long-term signals stability in four rear-edge populations from southern Spain. We demonstrate that, over recent decades, local climatic conditions have modulated the response of *J. sabina* secondary growth to the ongoing climate change. We observed a negative effect of winter-spring moisture on secondary growth that suggests a limitation for earlier growth activity at higher elevation, potentially hindering the ability of *J. sabina* to compensate forthcoming increases in summer drought. At the driest site, we also detected a positive effect of October precipitation, suggesting a second growth pulse by early autumn. Our results provide an example of how local climatic conditions may limit plastic responses of secondary growth to climatic variability. The implications of growth limitation in *J. sabina* exceed the species-scale level, since these prostrate shrubs play a critical role as nurse plants and local biodiversity foci in Mediterranean mountains.

1. Introduction

Climatic change is a major concern in Mediterranean mountains, where high diversity levels are threatened by faster than average rise in mean temperature (Giorgi and Lionello, 2008). Current climate in Mediterranean mountains combines low temperature with water shortage during summer, which implies an additional climatic constraint in relation to other alpine environments (García-Cervigón et al., 2012). Not surprisingly, plant growth in Mediterranean mountains usually shows a tighter response to changes in water availability than to temperature (Martín-Benito et al., 2010). In this water-limited scenario, the positive effect of global warming theoretically expanding the growing season length may be counterbalanced by rising drought stress, leading to potential growth declines and even mortality events (Olano et al., 2017).

Plant vulnerability to global warming has been considered higher in the rear edge of species distribution, where warmer conditions occur (Allen et al., 2010; Sánchez-Salguero et al., 2012). Nevertheless, this perspective has been challenged. Local adaptation may have shifted rear populations' tolerance to warmer (and drier) conditions, thus showing similar risk to global warming than core populations (Bennett et al., 2015). Also, rear-edge populations might maintain higher genetic diversity than core populations given their particular relationships with glacial refuge areas (Provan and Maggs, 2012). This evidence confers high conservation value to rear-edge populations for preserving whole species' range. Therefore, evaluating the effects of climate on rear-edge populations within Mediterranean high mountain ecosystems comes up mandatory to understand species future under global change.

Prostrate shrubs from the genus *Juniperus* are dominant woody species above tree line in Mediterranean mountains. Apart from being key landscape elements, these large shrubs also play a relevant role in shaping the structure of alpine plant communities by acting as nurse

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plants (Verdú and García-Fayos, 2003; García-Cervigón et al., 2013, 2015). Nurse plants act as shelter for other species, expanding their realized niche and ultimately increasing their distribution areas (Bulleri et al., 2016). As a result, a thorough understanding of nurse plant responses to global warming is critical to forecast expected trends at the community level (Rumpf et al., 2018). In this study, we explored the effects of climate warming on the secondary growth of the prostrate shrub *Juniperus sabina* L. along its southern distribution range in the Iberian Peninsula, where it grows isolated in a few mountain summits. Previous dendrochronological surveys with this species in other Iberian mountains have shown its potential for modifying secondary growth phenology to take advantage of the climatically favorable periods (Arzac et al., 2016). Otherwise, xylogenesis in Mediterranean conifers may be partly arrested during the summer drought period, recovering high cambial activity in autumn when conditions become cooler and wetter (Camarero et al., 2010). This plastic behavior would allow *J. sabina* to grow under harsh conditions above the tree line and would facilitate their populations to remain stable or even expand beyond its current distribution limits. However, a detailed evaluation of secondary growth responses to climate in rear-edge populations is still needed to confirm this potential geographical stability.

Our aim was to evaluate the main climatic factors driving secondary growth in rear-edge populations of *J. sabina*, as well as the time-related stability of climate sensitivity over the last decades. We hypothesized that (1) warmer conditions during spring will lead to an earlier initiation of secondary growth (Deslauriers et al., 2008), (2), precipitation during winter and early spring will pose a trade-off effect, since a thicker snowpack boosts soil water recharge during spring, while a thicker snow layer may cover junipers for a longer period, delaying the onset of cambial activity and leading to shorter growth seasons (Pellizzari et al., 2014, 2017), and (3) growth will depend on late spring and summer precipitation. We expected shifts in the relevance of climatic limiting factors along the studied period due to warmer temperatures and the subsequent increase in drought. Specifically, we expected an advanced effect of spring temperature on secondary growth due to earlier cambial activation, as well as more intense and earlier late spring climatic signals due to the earlier initiation of the drought stress period.

2. Material and methods

2.1. Study species and study area

Juniperus sabina (Savin juniper) is a long-lived shrub dwelling in mountains from western Europe to eastern Asia (Wesche and Ronnenberg, 2004; Adams et al., 2017). This prostrate shrub usually inhabits alpine environments, but may be also found in lower areas, where it colonizes pastures and agricultural fields after changes in land use (García-Cervigón et al., 2017). Field sampling was conducted in eastern Andalusia, south eastern Spain, where we selected four populations located along a 250 km gradient comprising the species' southwestern distribution range (Fig.1; Table 1). Sampling areas were located above the tree-line in Sierra de las Nieves (36º 41'N, 5º 01'W, Málaga province, Nieves hereafter), Sierra Mágina (37º 44'N, 3º 26'W, Jaén province, Magina hereafter), and Sierra Nevada (37º 05'N, 3º 22'W, Nevada hereafter) and Sierra de la Sagra (37º 57' N, 2º 33'W, Sagra hereafter), both situated in Granada province. Elevation ranged from 1914 m in Nieves to 2876 m in Nevada.

Study sites share high annual precipitation that is associated to oceanic western fronts. Precipitation declines as the exposure to these fronts is reduced, from a maximum in coastal and western mountains (1665 mm y^{-1} in Nieves) to a minimum in the inner and eastern areas (843 mm y^{-1} in Sagra). Despite the high annual precipitation, an intense summer drought occurs in all mountains when Azores High blocks western fronts, lasting from two to four months (from June-July to August-September). Frost period is long and can extend from October to May. As a result, the spring-summer period with both adequate temperature for xylogenesis (> 8 °C; Deslauriers et al., 2008; Rossi et al., 2008) and positive water balance conditions is short, ranging between one and two months (Fig. 1).

2.2. Climatic data

Climatic data for the period 1961–2010 were obtained for a 1.1 km^2 grid from Vicente-Serrano et al. (2017) and plotted using the *climatol* R package (Guijarro, 2016). High-quality climatic data from Mediterranean high mountains are scarce, and when interpolated data do exist (e.g. from the Climatic Research Unit), they may not adequately reflect the climatic conditions in these environments. In high mountain summits, temperature can be easily interpolated given the known increment of temperature with elevation. But interpolating rainfall is challenging due to the particular features of the Mediterranean climate and to the lack of local climate stations along the altitudinal gradient. In fact, sporadic rains can occur in summer, potentially having a strong impact on secondary growth (see Camarero et al., 2010). Therefore, we restricted our climatic analysis to the 50-year period from which high-quality climatic data were available. We also obtained the Standardized Precipitation Evaporation drought Index (SPEI) from Vicente-Serrano et al. (2010). These authors obtained the reference evapotranspiration used to calculate the SPEI by means of the Hargreaves equation (Hargreaves and Samani, 1985) using maximum and minimum temperature and the extraterrestrial solar radiation.

2.3. Field and laboratory work

Sampling was carried out in March–July 2011. At each site, we selected 35–40 juniper individuals and sawed a wood disk from a central branch (Fig. 2) at approximately 10–20 cm height from the soil surface. In the lab, wood disks were polished using sandpapers of increasing grit until the cellular structure could be seen. Afterwards, two radii per disk were selected and visually cross-dated, and ring widths were measured using a Velmex sliding stage micrometer interfaced with a computer. Cross-dating quality was checked using the COFECHA software (Grissino-Mayer, 2001). For standardization, raw series were fitted to a spline function with a 50% frequency response of 32 years, which was flexible enough to reduce the non-climatic variance by preserving high-frequency climatic information (Cook and Peters, 1981). Residuals obtained by dividing each raw ring width by its fitted spline value were pre-whitened by autoregressive modeling, giving dimensionless indices that represent independent records of annual growth for each measured series. Growth indices were averaged on an annual basis into a site chronology using a bi-weight robust mean. Ring-width series were detrended, standardized and averaged with the ARSTAN computer program (Cook and Holmes, 1996). First order autocorrelation (AC1), mean sensitivity (m_{sx}), mean inter-tree correlation (r_{bt}), signal-to-noise ratio (SNR), and expressed population signal (EPS) were obtained to assess chronology properties.

2.4. Statistical analyses

To assess changes in thermal conditions in the last decades, we regressed mean annual temperature and June-July evapotranspiration against time for each study site during the 1961–2015 period. Then, to identify relationships between climate and secondary growth, we obtained Pearson's correlations between residual ring-width chronologies and monthly climatic variables (precipitation and maximum temperature) for the common period 1961–2010, according to the period in which high quality climatic data were available. These correlations were calculated for a time window comprising from previous September to October of the growth year. We also obtained Pearson's correlations between residual ring-width chronologies and SPEI measured at weekly intervals from previous September to October of the

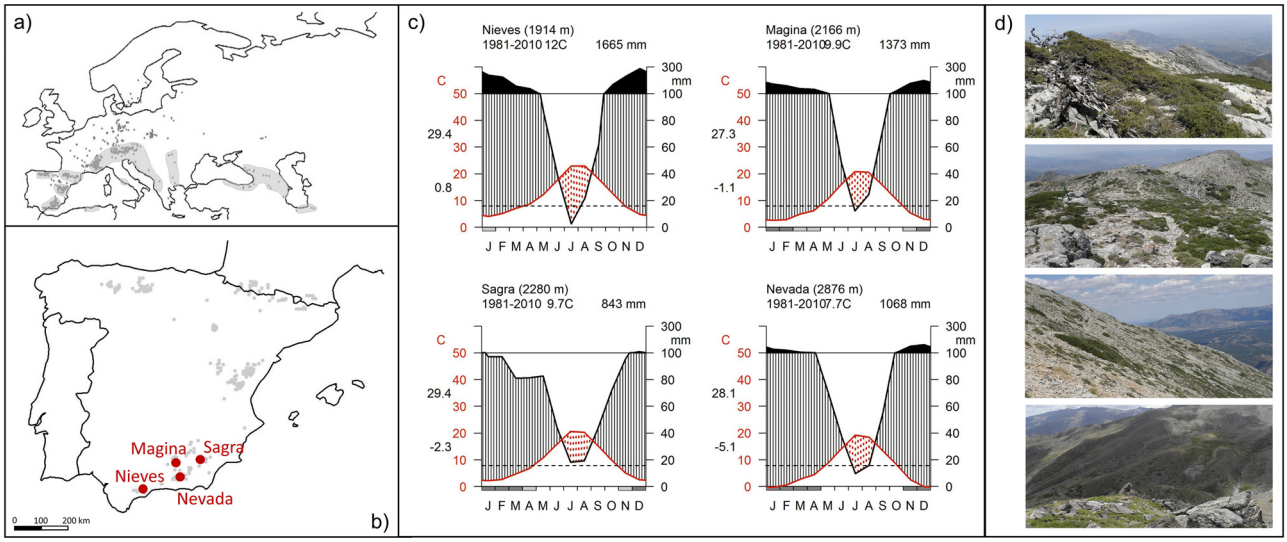

Fig. 1. Distribution of *J. sabina* in Europe (a) and Spain (b), location of sampling sites in south eastern Spain (b), climatic diagrams (c) and pictures of the four study sites (d). The European distribution map combines occurrence data from GBIF (points) and from Adams et al. (2017; grey areas). Occurrence data from GBIF are also shown in panel b (grey points). Dashed horizontal lines in climatic diagrams indicate the temperature threshold for xylogenesis, according to Deslauriers et al. (2008). Pictures from top to down correspond to Nieves, Magina, Sagra and Nevada study sites, respectively.

growth year at different timescales (lags of 1, 3, 6, 9 and 12 months). Finally, we performed 25-year moving correlations between residual ring-width chronologies and monthly climatic variables (precipitation and maximum temperature) from the most sensitive period (spring-summer) to assess changes in the intensity and timing of climate-growth relationships since 1961.

3. Results

Mean annual temperature showed significant warming over the 1961–2015 period in all study sites, ranging from +0.45 °C per decade in Magina to +0.22 °C in Nevada (Fig. 3a). Potential evapotranspiration in June-July increased accordingly (Fig. 3b), albeit with lower intensity, ranging from + 1.5 mm per decade in Magina to + 1.1 mm in Nieves.

The studied *J. sabina* populations yielded reduced secondary growth rates (Table 1), ranging from an average annual ring width of 0.341 mm y^{-1} in the fastest growing population (Magina) to 0.293 mm y^{-1} in the slowest one (Sagra). Year-to-year autocorrelation was moderate (0.536 in Magina to 0.371 in Sagra), while mean sensitivity was on average low (0.205 in Nieves to 0.138 in Magina). All populations had adequate EPS values for the studied time period (i.e., equal or higher than 0.85). Residual chronologies showed mid to low inter-site correlation for the 1961–2010 period (Table 2, Fig. 4). Sagra and Magina were the most correlated chronologies (r = 0.49), whereas Nieves and Nevada showed the lowest correlation (r = 0.28).

Climate-growth correlations revealed similar responses across sites, although with some differences (Fig. 5). In general, warm temperatures and low precipitation in spring favored secondary growth, although the exact timing of signals depended on the site. Nevada and Magina showed a stronger signal in May, with a negative effect of precipitation in both sites and a positive effect of maximum temperature in Nevada. In contrast, precipitation in March and March-April had a negative effect on growth in the lowest locality (Nieves), where positive effects of March and March-April maximum temperature were also detected. No significant correlations were found in Sagra for this period, but correlations in March were also negative with precipitation and positive with temperature. Higher growth was also associated with wet summer conditions in June (Nieves) and July (Sagra). This result implied a sharp change of the effects of precipitation and temperature from March-April to June-July, supporting the existence of a double climatic constraint, as regards spring low temperature and summer water shortage. This shift was also evidenced by the correlation between secondary growth and one-month lag SPEI in all sites (Fig. 6), especially in Sagra and Nieves. Overall, wet winter conditions and high spring SPEI values resulted in lower growth. Although this effect could be appreciated at different temporal lags and with different intensity, the best correlation was observed in one-month lag in all sites. Wet summers (June-July) favored secondary growth in Nieves and Sagra, where an additional positive effect of October conditions was also detected.

Climate-growth relationships were not stable over the study period. Moving correlations for spring and summer climatic variables (March-July) displayed consistent trends across sites (Fig. 7). June rainfall favored secondary growth in all sites, thus appearing as a limiting variable, whereas June temperature effect shifted from positive to neutral, becoming even negative in Nieves and Sagra. In contrast, changes in spring climatic conditions (i.e., at the onset of the growing season) showed no consistent patterns, although a release of climatic control in the last decade could be detected in Nieves and Sagra.

Table 1
Summary of ring-width chronology statistics for the period 1961–2010 at the four study sites.

Site	Time span	Average age (yrs.)	Plant/radii	RW (mm)	AC1	m_{sx}	r_{bt}	SNR	EPS
Nieves	1834–2010	123	19/42	0.312	0.431	0.205	0.315	8.75	0.897
Magina	1850–2010	130	32/43	0.341	0.536	0.138	0.189	7.46	0.882
Sagra	1786–2011	125	22/31	0.293	0.371	0.184	0.320	9.89	0.908
Nevada	1870–2010	109	17/27	0.318	0.43	0.182	0.248	5.60	0.848

Time span: full period covered by raw data. Plant/Radii: number of plant/radii used in the chronologies, RW: ring width, AC1: first-order autocorrelation of raw data, m_{sx}: mean sensitivity, r_{bt}: mean between-trees correlation, SNR: signal-to-noise ratio, EPS: expressed population signal.

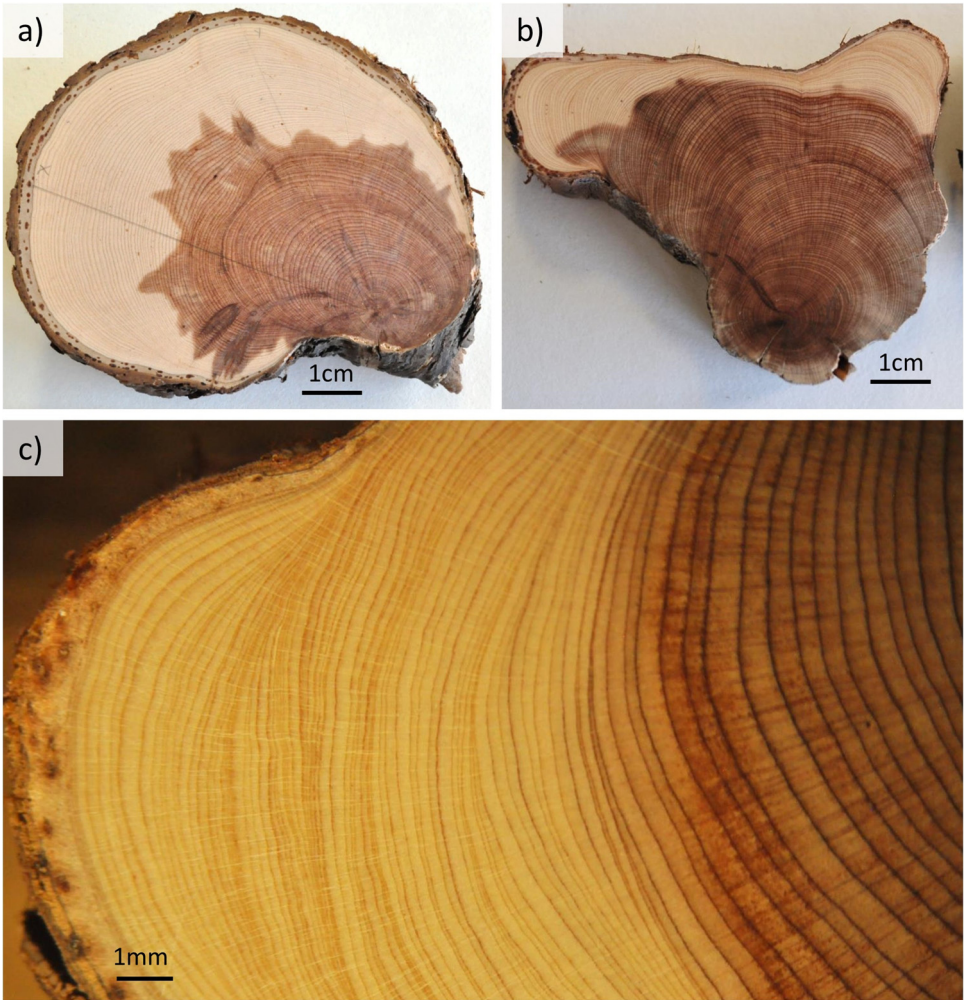

Fig. 2. Example of analyzed branch sections of *Juniperus sabina*. Individuals from (a) Sierra Nevada and (b) Mágina. Note that secondary growth is not concentric in these samples; instead, cambial activity is only maintained in some areas. (c) Detail on sapwood growth rings from the Mágina individual.

4. Discussion

Secondary growth in *J. sabina* revealed a robust climatic signal in its southern distribution range in Andalusia, south eastern Spain. Growth was favored by the same sequence of climatic variables in the four study populations, that is, dry and warm springs followed by wet and cool conditions in early summer. Nevertheless, climatic signals were not stable over time. Water limitation at the onset of summer drought became more intense and occurred earlier in the last decades, whereas only minor changes in the impact of early spring conditions (i.e., during the onset of secondary growth) were observed. This change of climatic constraints over time suggests an asymmetric effect of the recent warming trends on cambial activity of *J. sabina*, as has been observed across an altitudinal gradient in another Iberian mountain (Arzac et al., 2016).

4.1. Features of ring-width chronologies in the prostrate shrub J. sabina

The low secondary growth rates observed in the four study populations mimicked those previously found in other studies with the same species (García-Cervigón et al., 2012; Arzac et al., 2016). The fastest growing population (Magina) was the one showing the lowest inter-tree correlations. This low inter-individual correlation may indicate higher inter-individual variability related to lower climate harshness, as suggested by its highest growth rates. Besides, the effect of local perturbation patterns, like grazing and pollarding, might also explain these low inter-tree correlations. However, this hypothesis seems unlikely, since all the study sites share a similar land-use history in the recent past, when the intense human pressure in Mediterranean mountains was progressively reduced during the last decades (Lasanta-Martínez et al., 2005) until the inclusion of almost all sites (except Sagra) within protected areas. Nevertheless, EPS values in all study sites were sufficiently high to allow an adequate reliability of climate-growth analyses.

4.2. Effects of late-winter and early-spring conditions on secondary growth

Late winter and early spring (February-March) precipitation events negatively impacted secondary growth in *J. sabina*. It should be noted that precipitation in winter and spring plays contrasting roles in alpine and arctic environments, ranging from negative effects in areas where precipitation and snow cover are abundant (Franklin, 2013) to highly positive effects in semi-arid mountains (Olano et al., 2017). These contrasting effects result from the complex interaction between snow cover and plant growth. Snow cover insulates plants from extreme frost events (Hallinger et al., 2010) and maintains higher soil temperature, improving plant nutrition by increasing soil microbial activity (Schimel et al., 2004; Blok et al., 2015). These effects are especially relevant in small-statured or prostrate species such as *J. sabina*, which can remain completely covered by snow during most part of the winter. Moreover, in water-limited environments, snow melting maintains soil moisture during the initiation of summer drought (Walker et al., 1994; Giménez-Benavides et al., 2007). Juniper photosynthetic activity shows a highly

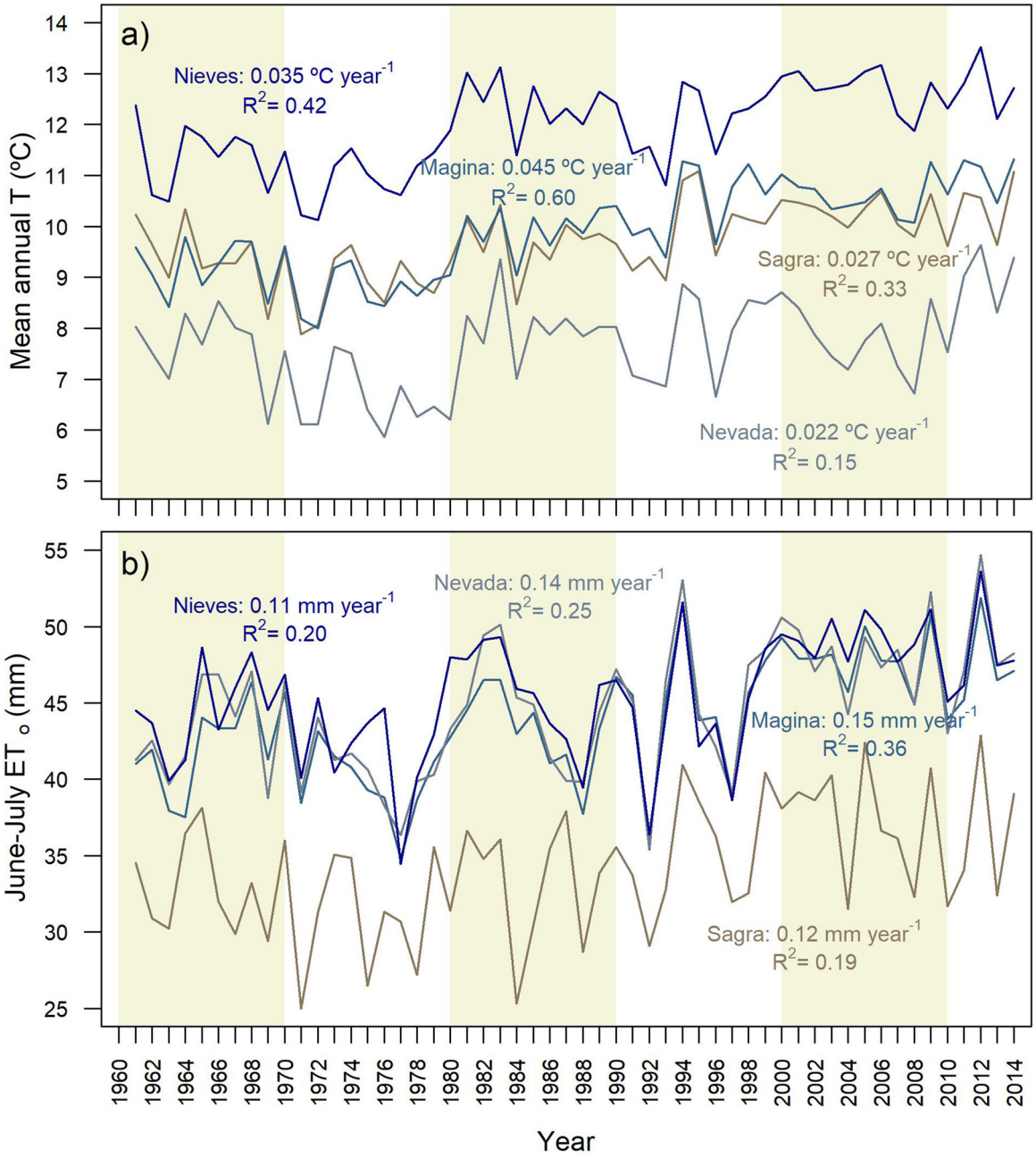

Fig. 3. Positive trends in mean annual temperature (T, a) and June-July potential evapotranspiration (ET_0, b) for the study sites. All correlations are significant at $P < 0.01$.

Table 2
Correlation matrix obtained by relating residual ring-width chronologies for the period 1961–2010. Values are Pearson correlations and significance levels are shown between parentheses.

	Nieves	Sagra	Magina
Sagra	0.480 (0.001)		
Magina	0.294 (0.038)	0.489 (0.001)	
Nevada	0.285 (0.045)	0.471 (0.001)	0.386 (0.006)

opportunistic behavior, as carbon gain can occur in winter if daily temperature rises over a certain threshold (Gimeno et al., 2012); this improved winter carbon uptake may be later allocated to secondary growth in early spring once snow melts (DeSoto et al., 2016). Notwithstanding, late-winter precipitation events are usually linked to cloudy conditions and lower daytime maximum temperatures, potentially exerting a negative impact on subsequent secondary growth. The existence of this negative effect of late winter precipitation can be inferred from the negative correlation observed between SPEI and growth in our study sites during late winter, before cambial activity initiation.

Warm and dry conditions before the onset of cambial activity were associated to higher growth. Temperature in high mountains constrains secondary growth initiation, leading to short growing seasons (Wipf and Rixen, 2010). High snowfall cover may also have an additional negative effect by delaying the achievement of adequate temperatures for cambial activity in stem tissues (Kirdyanov et al., 2003). Early cambial initiation allows a longer growing season with significant impact in final ring width (Lupi et al., 2010). This factor is critical in environments with very short growing seasons, such as alpine environments, but also under Mediterranean climates, where growth season length is arrested by summer drought (Camarero et al., 2010).

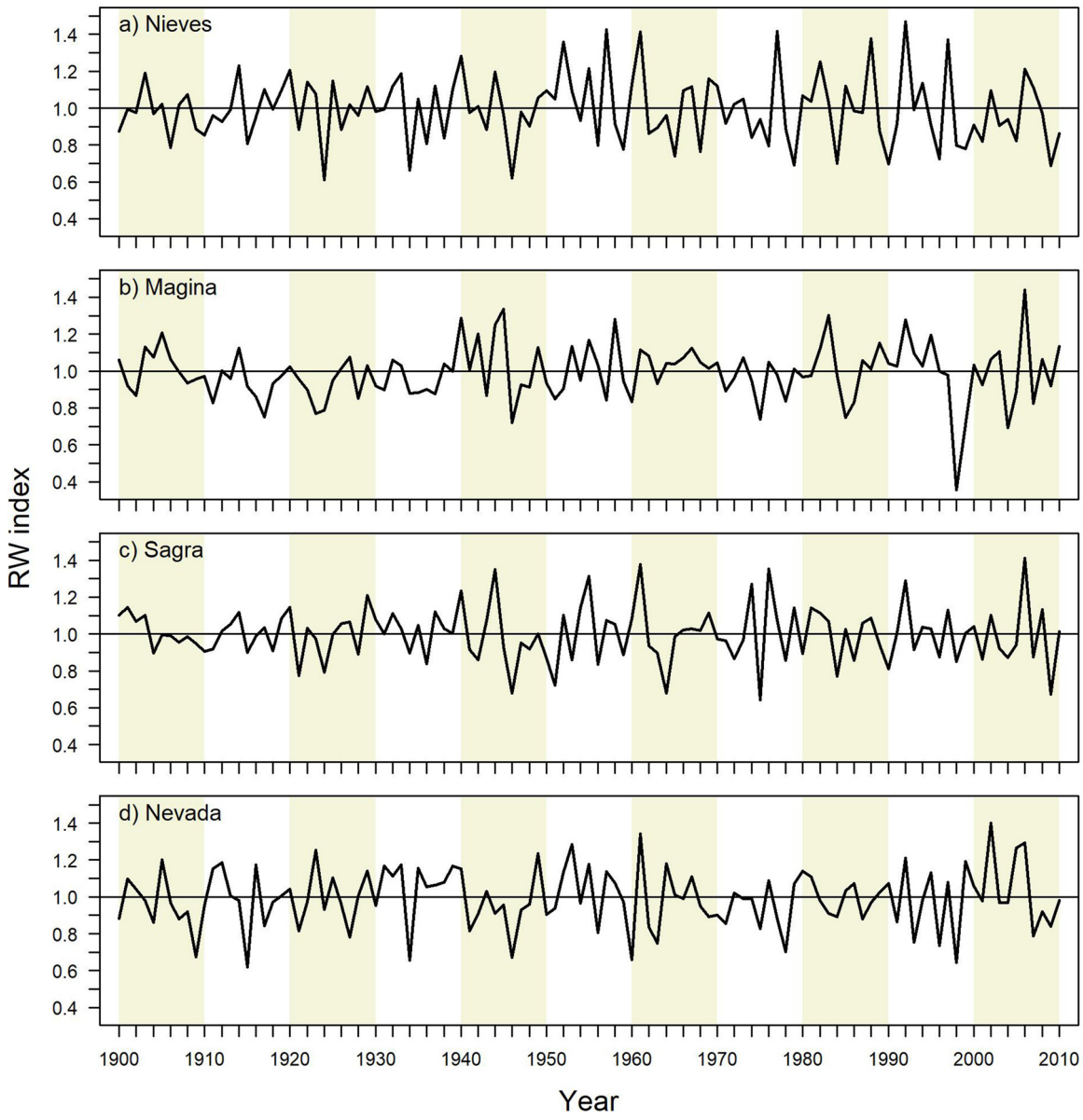

Fig. 4. Residual chronologies showing ring-width (RW) indices for the period 1900–2010 at the four study sites.

An earlier achievement of the threshold for xylogenesis (Deslauriers et al., 2008; Rossi et al., 2008; Li et al., 2016; Ren et al., 2018) seemed the most critical factor in our study sites, given the strongest correlations with climatic conditions observed in March-May, when this threshold is achieved. However, this signal was complex, since the positive effect of temperature was associated with a negative effect of precipitation, departing from the common signal observed in other water-limited juniper environments where spring precipitation has neutral (García-Cervigón et al., 2012) or even beneficial effects (Pellizzari et al., 2017). In fact, the negative effect of precipitation in Magina was higher than the positive effect of temperature. This signal may respond to the regional climatic pattern: western fronts bring significant amounts of precipitation during most of the year, particularly in winter and spring, but the Azores High blocks Atlantic fronts from late spring to autumn, causing persistent summer drought. Thus, excessive spring precipitation linked to cloudy and cool conditions may delay the achievement of suitable temperature for cambial activity or reduce the rate of cambial cell division in the first part of the growing season (Begum et al., 2013).

4.3. Summer and autumn climate signals

Higher water availability in early summer promotes secondary growth in drought-prone Mediterranean ecosystems (Camarero et al., 2010). In our study sites, summer drought led to a very short period of favorable climatic conditions (1.5 to 2.5 months, see Fig. 1). Drought was furthermore exacerbated by the shallow and rocky soils occupied by juniper, particularly in Nieves and Nevada sites, which might cause rapid soil water depletion. Then, maintenance of cambial activity becomes strongly linked to short-term precipitation, as shown by the rapid shift of SPEI signal from negative to positive signal in June (May in the lowest locality). A positive signal of precipitation combined with a negative effect of temperature is commonly reported in arid mountains, but also in Mediterranean forest ecosystems overall (Pasho et al., 2011) and diverges from the positive link between summer temperature and secondary growth characteristic of alpine and arctic tundra environments (Kirdyanov et al., 2007; Myers-Smith et al., 2015; Francon et al., 2017; Christiansen et al., 2018).

Wet October conditions were associated to higher growth at the driest site (Sagra), yet the other populations did not show this autumn-

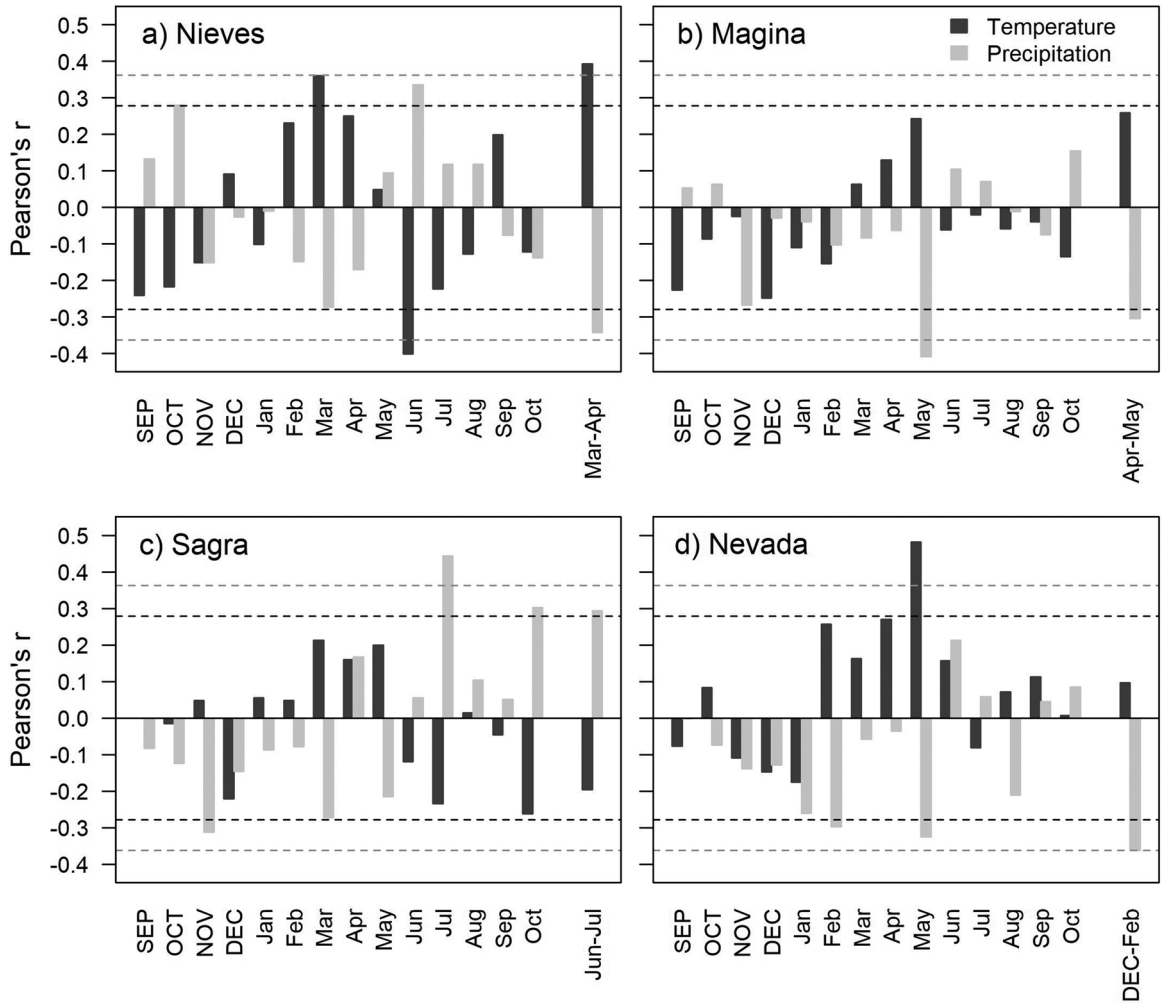

Fig. 5. Correlations calculated between residual ring-width chronologies and monthly maximum temperature (dark bars) and precipitation (light bars) at the four study sites. Correlations were performed in a temporal window comprising from September of the previous growing season (in capital letters) to October of the current growing season. Periods with highest correlations are also shown in the right-hand bars. Horizontal dashed lines indicate significance thresholds at $P < 0.05$ (dark) and $P < 0.01$ (light).

related climate signals. Cambial activity reactivation after summer arrest is a common feature of Mediterranean environments (Camarero et al., 2010), but low temperatures may hamper it in Mediterranean mountains (Arzac et al., 2016). However, positive signals of October SPEI and precipitation suggest a secondary growth pulse in wet autumns at the driest site, while coastal influence in the southernmost populations (Nieves) might allow extended growing seasons during summer.

4.4. Variations in climate-growth relationships over time

Climate-growth relationships were not stable over the study period. Increasing temperatures and higher evapotranspiration rates during last decades promote an earlier initiation of summer drought stress in Mediterranean ecosystems (DeSoto et al., 2012; Arzac et al., 2016). This effect could also be observed in our study sites, as supported by the shifting impact of June temperature from positive in the 1960s at the highest sites, to neutral or even negative, especially at the lowest site (Nieves). Simultaneously, wet June conditions became progressively more critical for secondary growth. Altogether, these signals suggest a temporal shift in those processes limiting cambial activity and increased dependence of secondary growth on late spring-early summer water availability. At once, the impact of climatic conditions at the onset of the growing season remained nearly constant, and only slight releases from climatic control could be detected, especially at the end of the study period.

4.5. Conclusions

Warm conditions in late winter and early spring favor an earlier initiation of secondary growth in southern populations of *J. sabina*, although abundant precipitation during this period may delay this earlier initiation. In addition, the maintenance of cambial activity becomes strongly linked to short-term summer precipitation, supporting the idea that summer drought strongly limits growth in this Mediterranean mountain species. The prevalence of very humid winter-spring conditions in southern Iberian mountains may therefore hinder the potential of this prostrate shrub to compensate forthcoming increases in summer drought stress with earlier growth activity. The implications of a decline in *J. sabina* populations exceed the species-scale level in two respects. On one side, this decline may negatively impact populations of protégée alpine plant species that benefit from growing beneath juniper canopies. But on the other side, the combined effect of persistent winter-to-spring moist conditions with strongest summer drought might ultimately result in even shorter growing seasons not only for *J. sabina*, but for other woody plant species inhabiting these singular ecosystems. The case of *J. sabina* therefore illustrates how idiosyncratic climatic conditions may affect the responses of woody

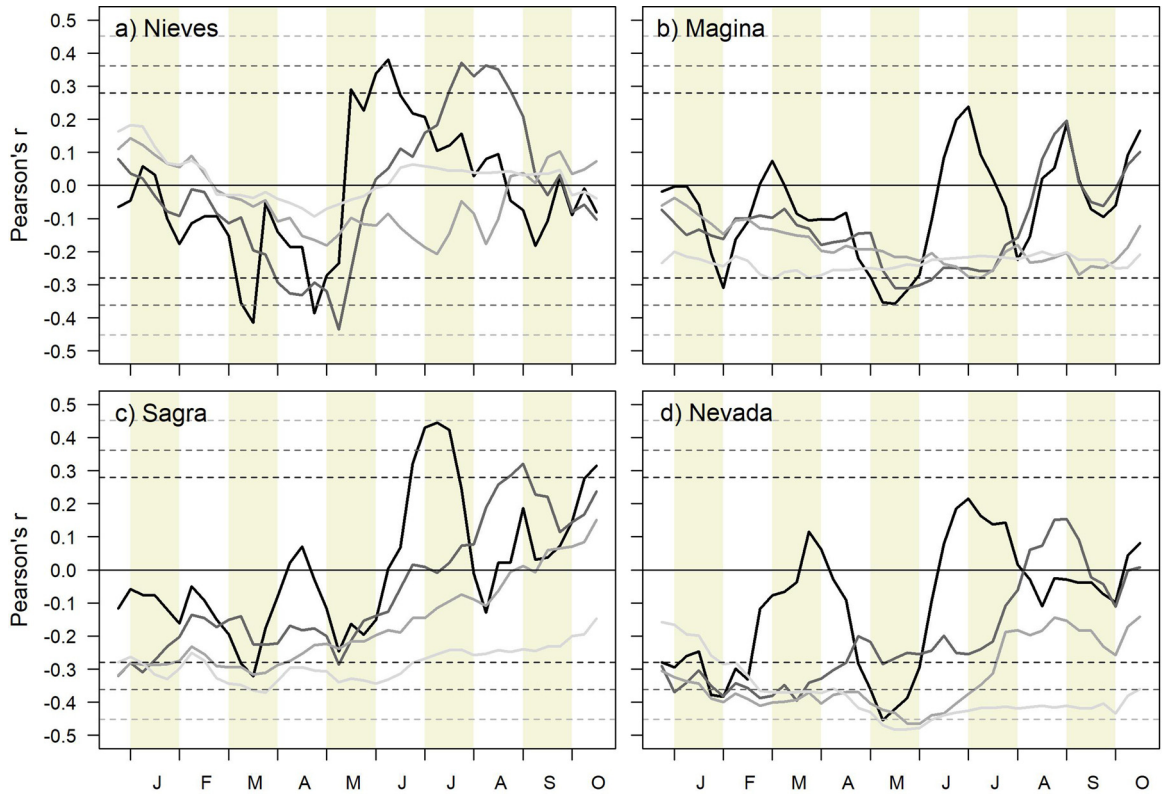

Fig. 6. Correlations between residual ring-width chronologies and SPEI values at temporal lags of 1 month (black), 3 months (dark grey), 6 months (grey), and 12 months (light grey). Data are calculated with a weekly temporal resolution (4 weeks per month). Horizontal dashed lines indicate significance thresholds at $P < 0.1$ (black), $P < 0.05$ (dark grey) and $P < 0.01$ (light grey).

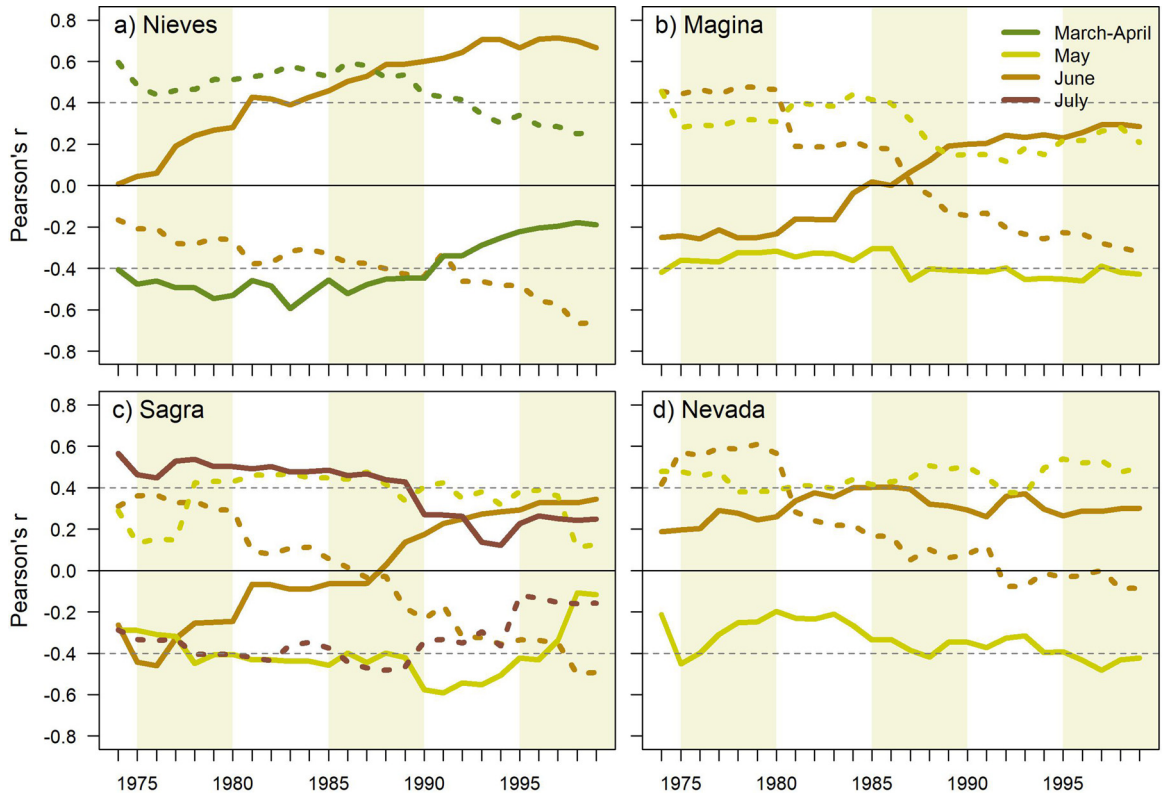

Fig. 7. Moving correlations between residual ring-width chronologies and the most significant climate variables at each site calculated at 25-year long intervals. Horizontal dashed lines indicate significance threshold at $P < 0.05$. Solid lines correspond with precipitation variables and dashed lines with temperature. Numbers in the x-axis indicate the central year of the moving average.

plants to the ongoing climate change in Mediterranean mountains.

Declarations of interest

None.

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